Taxonomic status of the Kinabalu 'linchi' swiftlet

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Swiftlets (Apodidae: Collocalini) are some of the most under-studied and taxonomical-ly difficult birds in the Old World tropics. The species are mostly small with drab black, grey or brown plumage, sometimes with white or gloss. Swiftlets are aerial insectivores and construct nests of their own saliva with or without exogenous material such as lichens, moss or feathers. Nests are placed in caves or below overhangs, such as cliffs or eaves of houses. Particular attention has been paid by taxonomists to the echo-locating swiftlets (*Aerodramus*), in part due to the commercial value of some species that construct edible nests (Francis 1987, Kang *et al.* 1991). *Aerodramus* presents difficult taxonomic problems because many species are cryptic and are distinguished only by the type of nest they construct or their geographic distribution (e.g., Medway 1966, 1975, Price *et al.* 2004). The other main group is the white-bellied swiftlets, *Collocalia*. Although there are fewer species of *Collocalia* *sensu stricto* than *Aerodramus* (three vs. 22; Chantler 1999), their taxonomy presents substan-tial challenges. The most widespread species, Glossy Swiftlet *C. esculenta*, spans an enormous range, from the Andamans and Nicobars in the Indian Ocean to the Solomons in the Pacific, and it exhibits substantial geographic variation, as suggested by its division into 32 subspecies (Salomonsen 1983, Chantler 1999, Dickinson 2003). Not only are the phyloge-netic relationships of many taxa within this polytypic complex unknown, particular confusion surrounds the relationship between Glossy and Cave Swiftlets *C. linchi* of the Indonesian archipelago. These two taxa are considered conspecific by some authorities (Inskipp *et al.* 1996, Smythies 1999) and separate species by others (Somadikarta 1986, Chantler 1999). The third *Collocalia* species, Pygmy Swiftlet *Collocalia troglodytes*, is clearly the sister of the other two (Price *et al.* 2004, Thomassen *et al.* 2005). To shed light on the rela-tionship between Glossy and Cave Swiftlets, we address an issue that is especially pertinent: the phylogenetic position of an enigmatic white-bellied swiftlet found in Sabah, Malaysian Borneo.

In 1905 a swiftlet was shot on the slopes of Mt Kinabalu in northern Borneo (elevation unknown) and described as *Collocalia dodgei* (Richmond 1905). In several respects, it resem-bled *C. esculenta*, the commonest swiftlet in both lowland and montane Borneo. Like *C. esculenta*, it had a whitish belly, but its dark upperparts exhibited a greenish gloss in con-trast to the bluish gloss of *C. esculenta*. (These glosses are both wear-associated differences.) It was also noticeably smaller and lacked the whitish tail spots and toe feathering common-ly found in *C. esculenta*. In 1937, two additional specimens were collected at 1,500 m on Mt Kinabalu and ascribed to *dodgei* based on their greenish gloss and small size. Cranbrook *et al.* (2005) described the history of subsequent taxonomic treatments of *dodgei*. Chasen (1935) merged *C. dodgei* as a subspecies of *C. esculenta*. For some years, there was confusion as to whether *dodgei* was the sole Bornean subspecies of *C. esculenta* (e.g., Smythies 1960), and eventually two subspecies were recognised in Borneo, *dodgei* on Mt Kinabalu and *cyanopti-la* over the rest of the island (e.g., Smythies 1981). This classification persists (e.g., Inskipp *et al.* 1996, Smythies 1999), but recent authors have acknowledged that parapatric (and possi-bly sympatric) occurrence of the two taxa on upper and lower slopes of Mt Kinabalu suggests the existence of distinct species. Indeed, Somadikarta (1986) reviewed the history

of white-bellied swiftlet taxonomy and, following an extensive examination of morphology and mensural data, concluded that *dodgei* was a subspecies of *C. linchi*, along with three other taxa: *linchi* on Java and the satellite islands of Madura, Bawean and Nusa Penida; *ripleyi* in montane Sumatra; and *dedii* on Bali and Lombok. This arrangement is commonly accepted (MacKinnon & Phillipps 1993, Chantler & Driessens 1995, Chantler 1999, Dickinson 2003) and solves the problem of parapatric or sympatric subspecies on Mt Kinabalu. The morphological distinction between *C. esculenta* and *C. linchi* is supported by molecular phylogenetic comparisons. Using two mitochondrial gene sequences, Price *et al.* (2004) found that an individual of *C. linchi* from Java appeared (with low bootstrap support) to be sister to *C. esculenta*, represented by subspecies from Malaya, Borneo, Philippines, New Guinea and the Solomons. Thomassen *et al.* (2003, 2005), also using mtDNA markers, recovered the same sister relationship between *C. linchi* and *C. esculenta*. Although Thomassen *et al.* (2003, 2005) used multiple individuals of *C. linchi* and *C. esculenta*, it is impossible to infer relationships among potential *C. linchi* taxa because the authors provided no subspecific names or locality information for their samples, nor did they discuss relationships within *C. linchi*.

The suggestion by Somadikarta (1986), on morphological grounds, that *dodgei* is a member of *C. linchi*, and the subsequent molecular demonstrations that *C. linchi* is the sister group of *C. esculenta*, solves the problem of parapatric (or sympatric) white-bellied swiftlets on Mt Kinabalu; they are members of different species. However, the question remains whether *dodgei* from Kinabalu is truly a member of *C. linchi* or a separate species. To address this issue, we obtained specimens of *dodgei* and *C. esculenta cyanoptila* from Mt Kinabalu and examined their evolutionary affinities using mtDNA sequences and morphological characters. For these comparisons, we not only produced our own DNA sequence data but also took advantage of the extensive mtDNA dataset published by Price *et al.* (2004), and the morphological data of Somadikarta (1986).

Materials and methods

We included three individuals of *C. esculenta cyanoptila* from *c*.1,500 m on the south side of Mt Kinabalu and two individuals of unknown identity (but presumably *dodgei*) from *c*.2,730 m, also on the south side of Mt Kinabalu. These two were nestlings close to fledging, with primaries still in the feather sheaths. The base colour of their upperparts is dark brown with a faint green gloss. Characteristic of *C. linchi*, their hind-toes lack the feather tuft found in *C. esculenta*, and their bellies are white, as opposed to the pale grey of *C. esculenta* taken at 1,500 m. The nest, found in the eaves of a hut, was a cup of rootlets, plant fibres and several types of lichens. It was attached to beams on two sides by hardened saliva.

DNA was extracted from muscle tissue using proteinase K digestion following the manufacturer's protocol (Dneasy tissue kit, Qiagen). For this study, we compared the entire second subunit of mitochondrial nicotinamide adenine dinucleotide dehydrogenase (ND2). Primers for the ND2 gene were L5215 (Hackett 1996), H6313, L5758 and H5766 (Johnson & Sorenson 1998). We purified PCR products with Perfectprep PCR cleanup kits (Eppendorf). Sequencing of purified PCR products was performed with BigDye Terminator Cycle Sequencing Kits (Applied Biosystems). Primers used for PCR were also used for cycle-sequencing reactions, resulting in bi-directional sequence for all taxa. Cycle-sequencing products were run on an ABI Prism 3130xl automated DNA sequencer (Perkin-Elmer Applied Biosystems). The computer programme Sequencher 4.7 (Genecodes) was used to reconcile chromatograms of complementary fragments and align sequences across taxa.

We analysed the data using maximum parsimony and maximum likelihood (ML) criteria in PAUP*4.0b10 (Swofford 2002). For ML analyses, Modeltest 3.7 (Posada & Crandall 1998) determined both the appropriate model of nucleotide substitution under the AIC criteria (see Posada & Buckley 2004) and the estimated parameter values. In parsimony analyses all characters were equally weighted. Support for nodes in the resulting phylogenetic hypotheses was assessed via non-parametric bootstrapping (Felsenstein 1985) and reanalysis of the resulting data (100 replicates).

Results

The aligned ND2 sequences yielded a matrix of 21 individuals (19 *Collocalia*, two outgroup *Aerodramus*) and 1,041 characters (Table 1). These included five individuals that we sequenced and 16 individuals from Price *et al.* (2004). All new sequences (GenBank EF600707–711) appeared to be mtDNA, rather than nuclear copies. They contained no stop codons, no conflicts in overlapping fragments, homogeneous base composition across taxa (chi-square $p=1.00$), expected codon-position divergences (3>1>2), and no unusual relationships amongst taxa. Base composition was biased towards adenine and cytosine (A=0.32, C=0.35, G=0.09, T=0.24) but consistent with other bird groups (e.g. Kirchman *et al.* 2001, Moyle *et al.* 2005).

Uncorrected pairwise divergences (*p*-distances) amongst taxa ranged from 0% between several pairs of individuals to 13.6% between *Collocalia troglodytes* and one outgroup taxon (Edible-nest Swiftlet *Aerodramus fuciphagus*). The two Kinabalu specimens had identical ND2 sequences, were 4.5% divergent from the Javan sample of *C. linchi*, and were 7.4–7.5% divergent from the three *C. esculenta* collected downslope from them on Mt Kinabalu.

Of 1,041 nucleotide positions, 118 were potentially parsimony informative. Modeltest (Posada & Crandall 1998) indicated a model of nucleotide substitution (TrN+G) that incorporated one class of transversions, two classes of transitions, and gamma distributed rates across sites. Parameter estimates for the data were as follows: base frequencies (0.332, 0.358, 0.090), rate matrix (1.0000, 37.4273, 1.0000, 1.0000, 26.2609), and shape (0.2168). Parsimony (nine most parsimonious trees of 444 steps with consistency indices of 0.694) and likelihood (one tree with -lnL = 3426.64578) analyses produced trees with no significant discrepancies (Fig. 1). Differences between our ML tree and that of Price *et al.* (2004) were minor and probably due to the latter's inclusion of an additional mitochondrial marker. *Collocalia troglodytes* was reconstructed as the sister of all other *Collocalia* sampled. *C. e. cyanoptila* from the Malay Peninsula and Borneo comprised a clade and only diverged from one another by a maximum of 0.7%. The only structure within that clade united the two Malayan individuals (Selangor) as distinct from the Borneo individuals. Sister to this large *cyanoptila* clade was a clade of four *C. esculenta* from the Philippines, two each from Sibuyan (*marginata*) and Mindanao (*bagobo*). Taxa from each island were monophyletic and supported as sisters by low ML bootstrap support (66) but high MP bootstrap support (88). The single individual of *C. linchi* from Java and the two Kinabalu birds formed a clade sister to Bornean and Philippine *C. esculenta*. Although the Javan and Kinabalu samples were substantially diverged from one another (4.5%), they were united as sister taxa with high bootstrap support (100 ML, 98 MP). A sister-pair of individuals from the far south-eastern portion of the *C. esculenta* range (New Guinea and Solomons) was sister to the clade comprising *C. linchi* and all other *C. esculenta* samples. Although the groups of taxa and geographic units (*C. linchi*, *C. e. cyanoptila*, Philippine birds, etc.) were well supported, bootstrap re-sampling indicated low confidence in the arrangement of these clades relative to one another.

TABLE 1

Samples included in the study. Source information: University of Kansas Natural History Museum, Lawrence (KUNHM); Field Museum of Natural History, Chicago (FMNH); Louisiana State University Museum of Natural Science, Baton Rouge (LSUMNS); and University of Washington Burke Museum (UWBM).

Species	Source	ID/Voucher	Locality
Aerodramus fuciphagus vestitus[1]	KUNHM	DMT027	Gomantong Caves, Sabah, Malaysia (Borneo)
Aerodramus maximus lowi[1]	KUNHM	DMT040	Gomantong Caves, Sabah, Malaysia (Borneo)
Collocalia troglodytes[1]	FMNH	358312	Sibuyan, Philippines
Collocalia esculenta bagobo (1)[1]	FMNH	357435	Mindanao, Philippines
Collocalia esculenta bagobo (2)[1]	FMNH	357440	Mindanao, Philippines
Collocalia esculenta marginata (1)[1]	FMNH	358301	Sibuyan, Philippines
Collocalia esculenta marginata (2)[1]	FMNH	358303	Sibuyan, Philippines
Collocalia esculenta becki[1]	UWBM	60227	Isabel Islands, Solomons
Collocalia esculenta nitens[1]	KUNHM	Msp068	New Guinea
Collocalia esculenta cyanoptila (1)[1]	KUNHM	DHC88	Lahad Datu, Sabah, Malaysia (Borneo)
Collocalia esculenta cyanoptila (2)[1]	KUNHM	DHC97	Lahad Datu, Sabah, Malaysia (Borneo)
Collocalia esculenta cyanoptila (3)[1]	KUNHM	DMT050	Sandakan, Sabah, Malaysia (Borneo)
Collocalia esculenta cyanoptila (4)[1]	KUNHM	DMT051	Sandakan, Sabah, Malaysia (Borneo)
Collocalia esculenta cyanoptila (5)[1]	KUNHM	DMT057	Selangor, Malaysia
Collocalia esculenta cyanoptila (6)[1]	KUNHM	DMT059	Selangor, Malaysia
Collocalia esculenta cyanoptila (7)	LSUMNS	B50298	Mt Kinabalu, Sabah, Malaysia (Borneo)
Collocalia esculenta cyanoptila (8)	LSUMNS	B50302	Mt Kinabalu, Sabah, Malaysia (Borneo)
Collocalia esculenta cyanoptila (9)	LSUMNS	B50304	Mt Kinabalu, Sabah, Malaysia (Borneo)
Collocalia linchi[1]	KUNHM	DHC72	Bogor, Java, Indonesia
Kinabalu swiftlet (1)	LSUMNS	B52699	Mt Kinabalu, Sabah, Malaysia (Borneo)
Kinabalu swiftlet (2)	LSUMNS	B52700	Mt Kinabalu, Sabah, Malaysia (Borneo)

[1] from Price et al. 2004.

Discussion

Molecular data indicate the monophyly of C. linchi populations embedded within C. esculenta (Thomassen et al. 2003, 2005; this study). Moreover, morphological characters, especially hind-toe feathering, small size and spotting on the rectrices, as well as sympatry of C. esculenta and C. linchi in Borneo and Sumatra, support the maintenance of C. linchi as a species separate from C. esculenta. The question remains, however, how to treat allopatric populations within C. linchi and C. esculenta. C. esculenta has a large range with numerous unsampled island populations and is in need of more detailed taxonomic work, which might elect to elevate a number of taxa to species status, but is beyond the scope of this study. There is, however, sufficient information on C. linchi populations to draw some conclusions as to their specific status.

C. linchi has a restricted, allopatric distribution on various Sundaic islands and has already been subject to extensive morphological study (Somadikarta 1986). Wing- and tail-length differences readily differentiate Mt Kinabalu specimens from all other populations of linchi (Table 2). In both dimensions, dodgei was found to be significantly smaller than the other three subspecies, and the range of its standard deviation did not overlap any of the others. Thus, morphology clearly delineates a disjunction between dodgei and other populations of C. linchi.

Molecular data also indicate the distinctiveness of dodgei. The uncorrected genetic divergence between the Kinabalu specimens and that from Java is 4.5%. This level of divergence is often found between species (e.g., Filardi & Moyle 2005, Sheldon et al. 2005) and

even genera of birds (Johns & Avise 1998, Whittingham *et al.* 2002). Although determining taxonomic rank solely on genetic divergence is problematic, this level of divergence never-theless indicates a long period of isolation between subspecies of *C. linchi*, sufficient to consider the Kinabalu population reproductively isolated and to be following an independ-ent evolutionary trajectory. This evidence, combined with significant differences in morphology, indicates that the Kinabalu form should be considered specifically as *Collocalia dodgei*, as originally described by Richmond (1905). We suggest Bornean Swiftlet as an appro-priate English name, rather than Kinabalu or Sabah Swiftlet, in view of the possibility that other populations may be discovered on other high mountains on the island (see below).

The recognition of *C. dodgei* adds yet another montane endemic to the list of Bornean birds. Depending on classification (Inskipp *et al.* 1996, Smythies 1999), about 33 of 41 Bornean endemics are montane or submontane in distribution (Sheldon *et al.* 2001: 15). This number includes not only *C. dodgei* but also the forktail, *Enicurus (leschenaulti) borneensis,*
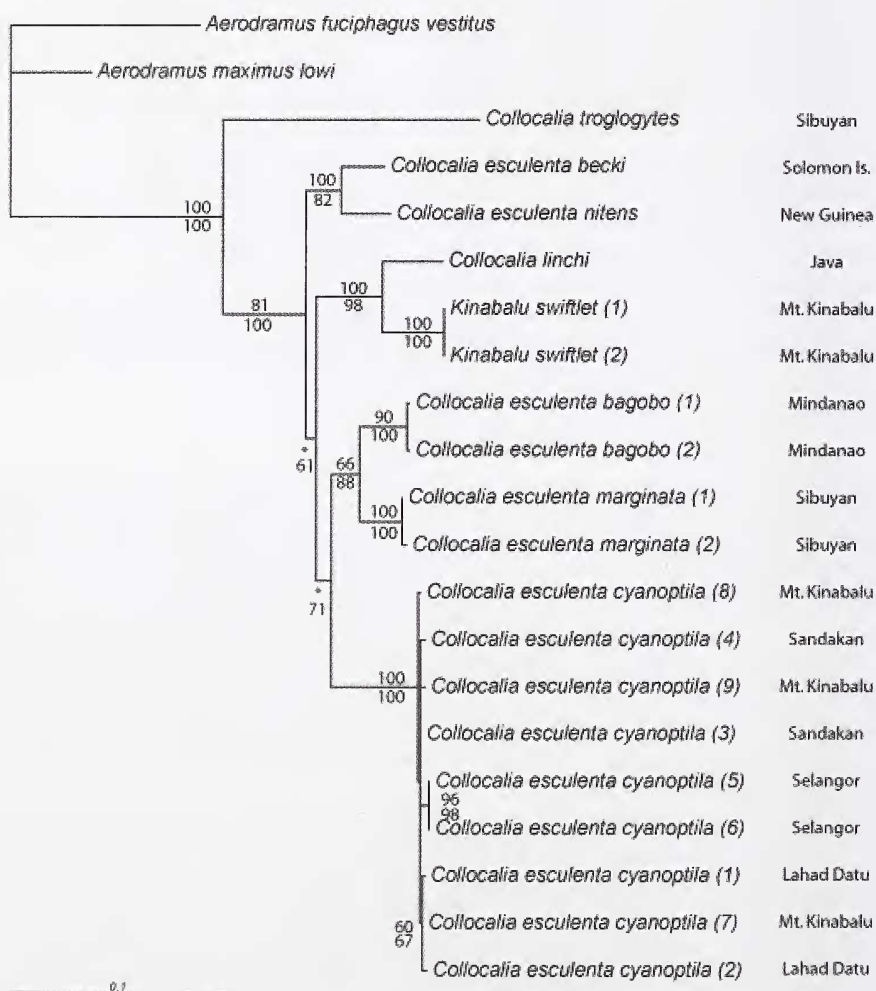

Figure 1. Maximum likelihood estimate of relationships among *Collocalia* swiftlets based on ND2 DNA sequences. Numbers by nodes refer to maximum likelihood/maximum parsimony bootstrap support. Asterisks or blank nodes indicate bootstrap support less than 50%. Numbers by names refer to Table 1. Branch lengths are proportional to the expected number of substitutions per site, as indicated by the scale bar.

TABLE 2

Wing- and tail-length data condensed from Somadikarta (1986). Values are mean ± standard deviation with the number of individuals in parentheses. All measurements are in mm.

Subspecies	Wing, mean ± SD (*n*)	Tail, mean ± SD (*n*)
dodgei	88.67±1.04 (3)	34.50±1.32 (3)
ripleyi	93.02±3.18 (25)	38.24±1.60 (25)
linchi	94.50±2.00 (77)	41.48±1.45 (58)
dedii	97.19±2.40 (45)	44.25±1.33 (40)

which like *C. dodgei* appears to be most closely related to taxa on Java rather than to low-land counterparts on Borneo (Moyle *et al.* 2005). Further study is likely to reveal close relationships between other Bornean montane taxa and species on the mountains of other Sundaic islands. Such inter-island phylogenetic connections suggest montane taxa were once widespread in the Sundas and that their speciation was caused by island vicariance and montane isolation rather than by intra-island mechanisms, such as displacement by invading species (Sheldon *et al.* 2001) or parapatric ecological separation (Smith *et al.* 1997, Cadena 2007).

BirdLife International (2004) lists *C. linchi* as Least Concern because of its large geo-graphic distribution (Java, Sumatra, Malaya, Bali and other small islands) and common occurrence in some areas. That the Bornean population is a separate species changes this sit-uation. The only known locality for *C. dodgei* (documented by just five specimens) is Mt Kinabalu. The two recent specimens were taken at 2,730 m, and these upper slopes are pro-tected by Kinabalu National Park. However, *C. dodgei* could easily occur on other Bornean mountains that are less protected and studied than Kinabalu. Appropriate habitat, for example, probably exists on nearby high peaks such as Mt Tambuyukon (2,579 m) and Mt Trus Madi (2,649 m). Surveys of the latter (Sheldon & Francis 1985, Moyle & Wong 2002) have found *C. esculenta* as high as 2,100 m, but have not recorded *C. dodgei*. However, swiftlets are notoriously difficult to identify in the field, and no specimens of *Collocalia* have been collected on Trus Madi, so *C. dodgei* could easily have been overlooked. If the species occurs there, or on Mt Tambuyukon, it would be near the summit, where the avifauna is especially poorly known.

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